Stay with the flow: How macroinvertebrate communities recover during the rewetting phase in Alpine streams affected by an exceptional drought

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Stay with the flow: how macroinvertebrate communities recover during the rewetting phase in Alpine streams affected by an exceptional drought

Short running title: Resilience of macroinvertebrates to droughts in Alpine streams

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Abstract

Drought occurrence is affecting an increasing number of lotic ecosystems worldwide due to the combined effects of climatic and anthropogenic pressures. Unlike naturally intermittent rivers, where the drying phase is a part of the annual flow regime, water scarcity in Alpine rivers represent a relatively recent phenomenon and, therefore, a major threat for the biodiversity of these lotic ecosystems, but the response of aquatic communities to this disturbance is still poorly investigated. Here, we present the results on the recovery of stream macroinvertebrates in two Alpine streams after a supra-seasonal drought. As water resumed, a total of ten sampling sessions were carried out and temporal patterns in diversity, density and taxonomic composition of benthic communities as well as in the percentage of functional feeding groups were investigated.

We found that the resistance of invertebrate communities in Alpine streams is generally low: drought significantly reduced the diversity and density of macroinvertebrates. Conversely, our results suggest that the passive dispersal by drift from the upstream river sections seems the main mechanism that promotes the post-drought recovery. Nevertheless, this resilience ability appears to be stream-specific and influenced by intrinsic stream characteristics, including the flow permanence and distance from the nearest upstream perennial reach. This work sheds light on the impacts of climatic and human-induced droughts on benthic invertebrate communities and assumes a primary importance to predict their future composition in relation to the intensification of flow intermittency in Alpine areas under the current global change scenario.

Keywords: benthic invertebrates, Alpine streams, water scarcity, recolonization, biodiversity, resilience

1. Introduction

Climate change is currently one of the most relevant challenges for habitat and species conservation worldwide because the raising in air temperature and alterations in the precipitation regimes are responsible for the habitat loss and fragmentation, changes in species phenology and enhanced rates of biodiversity loss (Dawson, Jackson, House, Prentice, & Mace, 2011; Mantyka-pringle, Martin, & Rhodes, 2012). The increased frequency and magnitude of hydrological extremes, such as floods and droughts, are among the main consequences of these phenomena for lotic ecosystems (Beniston, 2012; Heino, Virkkala, & Toivonen, 2009; Middelkoop et al., 2001; Ledger, & Milner, 2015; Whitehead, Wilby, Battarbee, Kernan, & Wade, 2009; Wu, & Johnson, 2019).

Alpine streams are expected to be extremely sensitive to the effects of droughts because the Alps are one of the most impacted areas by climate change and, at the same time, water abstraction is an increasing pressure (Fenoglio, Bo, Cucco, Mercalli, & Malacarne, 2010; Gorbach, Shoda, Burky, & Benbow, 2014; McKay, & King, 2006; López-Rodríguez, Márquez Muñoz, Ripoll-Martín, & Tierno de Figueroa, 2019). Under similar conditions, drought occurrence represents a major threat for stream macroinvertebrates, as documented by some authors (Bonada, Doledec, & Statzner, 2007; Calapez, Elias, Almeida, & Feio, 2014; Doretto et al., 2018b; Durance, & Ormerod, 2007; Fenoglio, Bo, Cucco, & Malacarne, 2007; Ledger, Brown, Edwards, Milner, & Woodward, 2013; Piano et al. 2019a; Pinna et al., 2016; Smith, McCormick, Covich, & Golladay, 2017; Storey, 2016).

A growing attention is paid by river ecologists on the resistance and resilience mechanisms of benthic organisms to face the drying phase (Chester, & Robson, 2011; Fritz, & Dodds, 2004; Robson, Chester, & Austin, 2011; Aspin et al., 2019). However, the resistance ability of aquatic invertebrates to drought in Alpine streams is generally considered limited, compared to the aquatic biota of other geographical regions, such as the Mediterranean area, where the drying phase is a natural part of the annual flow regime (Leigh et al., 2016; Tierno de Figueroa, López-Rodríguez, Fenoglio, Sánchez-Castillo, & Fochetti, 2013). Benthic communities in Alpine streams, therefore, are generally considered more resilient than resistant (Doretto et al., 2018b), but scientific evidence on this is still limited.

In a recent publication, Van Looy et al. (2019) developed a general framework to explain the resilience of aquatic communities to disturbance in streams, including droughts, based on the relative and combined role of three main drivers: resources competition and/or facilitation, recruitment and refugia. Firstly, the access or limitation to food resources affect the response of aquatic communities in terms of trophic and biotic relationships, acting as the major driver of the post-disturbance recovery especially where the energetic inputs are pulsed- or patchy-distributed (Richardson & Sato, 2015). In this context, ameliorative effects of large amount of organic matter on macroinvertebrate communities have been reported also in relation to other physical disturbances, such as siltation (Doretto et al., 2017). Second, recruitment (i.e. the gain of individuals by the dispersal from adjacent habitat sources) is expected to play a primary contribution in highly connected river networks, resulting in a faster post-drought recovery (Flower, 2004; Ledger & Hildrew, 2001). Finally, habitat heterogeneity promotes the presence of in-stream refugia (mainly pools and the hyporheic zone) that can be exploited by the benthic taxa, according to their ecological traits, to survive under drying conditions (Boulton 2003; Chester & Robson, 2011; Fenoglio, Bo, & Bosi, 2006; Otermin, Basaguren, & Pozo, 2002; Verdonschot, Oosten-Siedlecka, Braak, & Verdonschot, 2015; Wood, Boulton, Little, & Stubbington, 2010).

In this study we monitored the post-drought recovery of macroinvertebrate communities in two Alpine streams affected by a supra-seasonal drought (Lake, 2003) and discussed the results in relation to the contribution of food resources, recruitment and refugia. In particular, temporal patterns in composition and diversity of benthic invertebrate communities were evaluated during the water resumption (hereafter rewetting phase) and compared to the upstream permanent reaches. Our hypotheses were that: i) the invertebrate recruitment, especially in terms of recolonization by drift from the upstream sections would be the main mechanism of resilience in our streams, while ii) the resource availability would have a minor role. As the supra-seasonal drought was one of the most prolonged ever reported for the Italian Alps, lasting for more than 5 months, we expected a negligible effect of the in-stream refugia (i.e. pools and hyporheic zone). In addition, we postulated that the recovery process would be affected by stream-specific characteristics, especially in relation to hydrology stability and flow persistence.

2. Materials and methods

2.1 Area of study

The sampling area is located in the Cottian Italian Alps (Northwestern Italy), where we examined the post-drought recovery in two lotic systems, namely the Po and Pellice rivers, which originate at 2,022 and 2,387 m.a.s.l. respectively. The former is the longest Italian watercourse: it runs for 652 Km until the Adriatic Sea with a drainage basin of approximatively 71,000 Km^2. The latter is the principal tributary of the Po river within the Alpine area and runs for 55 Km (drainage area: 974 Km^2)

before its confluence (Fig. 1). They represent two good case studies as they have good water and biological qualities but with stretches recently affected by drought.

On each river, two sampling sites were selected: a perennial stretch (P), with permanent flow throughout the year, and an intermittent stretch (I) experiencing recurrent drought events since 2011 (ARPA, 2013; Piano et al., 2019a; 2019b), due to the joint effect of climate change and consequent water abstraction to fulfill human needs. At this scale of investigation, the Po and Pellice are 5-order rivers (Strahler, 1957), with the substrate dominated by coarse mineral elements and a pluvio-nival hydrological regime. Also, the land use is very similar between these two streams: more than 90% is represented by natural areas, while agricultural and urbanized areas on average account for 8% and 1.5% (Table 1).

2.2 Data collection

In 2017, Northwestern Italy experienced the most severe summer droughts ever reported. In the lower sections of the Po and Pellice rivers, including the intermittent sites here considered, surface water ceased in July and August 2017 respectively (Falasco, Piano, Doretto, Fenoglio, & Bona, 2018) and resumed only in January 2018, after conspicuous rainfalls (see Supplementary Materials Fig. SM1). Although a marked reduction of the river discharge, the upstream perennial sites were characterized by the continued permanence of running surface water during this period.

As water resumed, a total of ten sampling dates were carried out in the intermittent sites to monitor the post-drought recovery of benthic communities, covering a 3-month period (Table 2). To better describe the first phases of the recolonization process, samples were initially collected every 3 days, while at the end of the sampling period benthic invertebrates were sampled every two weeks. Moreover, since we expected that the upstream perennial stretches acted as sources of organisms during the recolonization process, macroinvertebrates were sampled also in the perennial sites on two selected occasions, namely on 19th January and 22th March 2018. These samplings allow to obtain an overview of macroinvertebrate communities, at the beginning and at the end of the studied period.

On each sampling occasion, dissolved oxygen concentration (mgL^{-1}), oxygen saturation (%), pH, water temperature (°C) and electrical conductivity (μScm^{-1}) were measured with a multiparametric probe (Hydrolab mod. Quanta). Water depth (cm) and water velocity (ms^{-1}) were measured for each sample using a flowmeter (Hydro-bios Kiel). Moreover, the composition of the substrate within the area delimited by the Surber sampler was visually estimated. Based on the Wentworth's grain size classification (1922), the percentages of boulders (>256 mm), cobbles (256-64 mm), gravel (64-2 mm) and fine sediment (<2 mm) were estimated by the same operator. Macroinvertebrates were collected using a Surber sampler (0.05 m^2, 250 µm mesh-size) and three samples were taken on each sampling occasion, with the only exception represented by 23th February, when no samples were collected in the intermittent site of the Po river because the stream bed was completely dry (Table 2). Samples were preserved in 70% ethanol and returned in laboratory for the sorting under a stereo-microscope. Specimens were counted and systematically identified to genus (Ephemeroptera and Plecoptera) or family level using the taxonomic keys for the Italian macroinvertebrate fauna (Campaioli, Ghetti, Minelli, & Ruffo, 1994; 1999), and also classified into functional feeding groups (FFGs: collector-gatherers, filterers, predators, scrapers and shredders; Merritt, Cummins, & Berg, 2008).

2.3 Statistical analyses

Significant differences in the environmental parameters between the perennial and intermittent sampling sites (i.e. Pellice I vs Pellice P and Po I vs Po P) as well as between rivers (i.e. Pellice and Po) over the monitored period were visualized by means of Principal Component Analysis (PCA) and tested with Permutational Analysis of Variance (PERMANOVA). The water temperature, pH, electrical conductivity, dissolved oxygen and the mean value of the water velocity, depth and percentage of the four substrate classes was calculated for each sampling site on each date and included in this analysis. To meet the assumptions of normality, percentage data were square-root(arcsin) transformed prior performing the PCA, which was run using the "prcomp" function in the basic package of R. The "adonis" function in the *vegan* R package (Oksanen et al. 2015) was used, instead, to perform the PERMANOVA analysis, for which the Euclidean distance was applied. Changes in the taxonomic composition of benthic communities between sampling occasions and sites were initially visualized by means of a Non-metric Multidimensional Scaling (NMDS). This multivariate analysis was performed using the function "metaMDS" in the *vegan* R package (Oksanen et al. 2015). Surber samples were used as separate replicates: raw data about the abundance of macroinvertebrates were square-root transformed and then a Bray-Curtis dissimilarity index was applied. PERMANOVA was run to test for significant differences in relation to the "time" (as days from the water return) and "site" (Pellice P, Pellice I, Po P and Po I) factors. Generalized Additive Models (GAMs) were used to assess the non-linear response of the community metrics over the time, expressed in terms of days from the water return. Prior to perform the statistical models, data exploration was carried out according to Zuur, Ieno & Elphick (2010) and outliers were removed. Four taxonomical metrics were considered: the total taxa richness, total density of macroinvertebrate (number of individuals m^{-2}) as well as EPT (Ephemeroptera, Plecoptera and Trichoptera) richness and density. In addition, the percentage of each functional feeding group and the ratio between scrapers and total collectors were also taken into account. The latter parameter has been proposed as an ecosystem indicator for the prevalence of autotrophy (i.e. grazing) or heterotrophy (i.e. detritus chain) in rivers (Cummins, Merritt, & Andrade, 2005). Samples collected in the perennial sites were not included in the regression models, but the mean value of each metric was calculated to better interpret the observed patterns.

All the GAMs were carried out using the "gam" function in the *mgcv* R package (Wood & Wood, 2015): a Poisson distribution was used for count data, while the negative binomial distribution was alternatively used in case of overdispersion. The binomial distribution was instead applied for the percentage variables. All the analyses were performed with the statistical software R (R Development Core Team, 2018).

3. Results

3.1 Environmental parameters

The first and the second axes of PCA accounted for 25.6% and 22.5% respectively of the variance associated to the environmental parameters, for a cumulative percentage equal to 48.1% (Fig. 2). The first axis (PC1) was positively correlated with the electrical conductivity and negatively correlated with the pH and water velocity. By contrast, the second axis (PC2) was positively correlated with the percentage of cobbles and the dissolved oxygen, while it was negatively correlated with the percentage of sand, water depth and water temperature.

In general, samples from the Pellice river were mainly oriented in the top-left part of the plot and showed a less pronounced dispersion, while samples from the Po river were oriented in the bottom-right part of the graph and showed a higher dispersion. Nevertheless, PERMANOVA did not show significant differences in the environmental parameters among sampling sites (P = 0.184) and rivers (P = 0.056), despite the p-value in this latter case was close to the significant threshold.

3.2 Macroinvertebrates

A total of 12,570 macroinvertebrates were collected, belonging to 38 different taxa (Supplementary Materials: Table SM1). Plecoptera, Ephemeroptera and Diptera were the orders with the highest number of taxa (8), followed by Trichoptera (6), Coleoptera and Oligochaeta (2), Odonata, Tricladida, Crustacea and Nematomorpha (1). In general, *Baetis* sp., *Rhithrogena* sp., Hydropsychidae, Chironomiidae and Simuliidae were the dominant taxa in the perennial and intermittent sites of both rivers. The average number of taxa per sample was 10, while the mean number of individuals per sample was 182.

Results of the NMDS and PERMANOVA analyses showed a significant effect of the factors "time" ($F_{9,45} = 3.311$; $P < 0.001$) and "site" ($F_{3,45} = 7.302$; $P < 0.001$) on the composition of macroinvertebrate communities (Fig. 3). Invertebrate samples collected in the intermittent site of the Pellice river (Pellice I) showed a similar taxonomical composition, as they clustered together in the central part of the plot. Moreover, a partial overlap with the composition of the upstream perennial site (Pellice P) was observed. On the contrary, macroinvertebrate communities in the intermittent site of the Po river (Po I) showed the highest dispersal indicating a significant variation in the taxonomic composition over the time. Samples from this site were mostly oriented in the left-side of the plot and did not overlap with samples collected in the upstream permanent site (Po P).

When looking at the temporal variation of the diversity and density of macroinvertebrates during the rewetting phase, we found significant differences between the two rivers (Table 3). Total richness in the Pellice river significantly increased over the time, from 8 to 14 taxa (Fig. 4a, Table 3), despite it was lower than that of the upstream perennial site (18 taxa). Conversely, the total richness in the Po river slightly increased within the first 20 days of rewetting and then it markedly dropped (Fig. 4a). The average number of taxa recorded in the intermittent and permanent sites of the Po river at the end of the study were 5 and 20 respectively.

Similar results were obtained for the EPT richness, which showed opposite trends in the two rivers (Fig. 4b, Table 3). The number of EPT taxa significantly increased since the water resumption and completely approached the same value of the upstream permanent site (10 taxa). By contrast, EPT richness progressively decreased in the Po river and at the end of the sampling period was quite lower than that in the upstream permanent site (11 taxa).

Significant temporal variations in the density of macroinvertebrates were also observed in both rivers (Table 3). In the Pellice river the total density of macroinvertebrates significantly increased over time, from 2,000 to approximatively 5,000 individuals m^{-2} after 73 days of rewetting (Fig. 4c). However, it was still lower than the average density recorded in the perennial section (7,700 individuals m^{-2}). Conversely, total density of macroinvertebrates in the Po river peaked around 25 days after the water resumption but then it collapsed (Fig. 4c). The numerical gap with the upstream site (6,400 individuals m^{-2}) was high, despite the increment on the last sampling occasion. As EPT taxa were numerically dominant in this study, the temporal variation of EPT density closely resembled that observed for the total density, especially in the Po river (Fig. 4d, Table 3). The EPT density in the Pellice river, instead, showed a sharp increase after 20 days from the water resumption and then stabilized around a value of 3,500 individuals m^{-2}, that was comparable to the average EPT density in the perennial site (4,290 individuals m^{-2}).

With exception of shredders, percentages of functional feeding groups significantly varied over the time (Table 3). On average, collector-gatherers were the most abundant group in the Pellice river (34%) followed by filterers (32%), despite these two groups showed some fluctuations (Fig. 5a). Also, the percentage of scrapers was high (29%) and relatively constant over the time (Fig. 5a), while a general increase was observed for predators during the rewetting phase but, on average, they accounted for less than 4%.

Benthic communities in the Po river were almost exclusively dominated by collector-gatherers (50%) and scrapers (40%): the former were more abundant on the first and last sampling occasions respectively, while the latter were numerically abundant on the intermediate sampling occasions (Fig. 5b). The percentage of filterers was generally low (8%), despite this functional group peaked after 31 and 45 days from the water resumption (Fig. 5b). Predators were recorded only on few sampling occasions in the Po river and no significant trends were observed for this group (Fig. 5b, Table 3). Most representative taxa of each functional feeding group are listed in Table SM1 (Supplementary Materials).

Changes in the ratio between the scrapers and total collectors (i.e. shredders, collector-gatherers and filterers) were observed only in the Po river, where this indicator rapidly increased during the initial stages of the rewetting phase, peaked around 20 days, and then it decreased at the end of the study (Fig. 5c, Table 3).

4. Discussion

In a review on the response of riverine communities to disturbance, Death (2010) pointed out that, in general, benthic communities recover rapidly because they are more resilient rather than resistant. In this study we monitored the post-drought recovery of macroinvertebrate communities after a supra-seasonal drought in two Alpine streams and our findings corroborate this statement.

Drought significantly reduced the diversity and density of invertebrate communities, especially regarding the most sensitive invertebrates, like EPT taxa, and confirmed our hypothesis for which the resistance of Alpine macroinvertebrates to this disturbance is quite scarce, as demonstrated previously (Doretto et al., 2017; Fenoglio et al., 2007; Herbst, Cooper, Medhurst, Wiseman, & Hunsaker, 2019; Piano et al., 2019a). Moreover, this limited resistance could be explained by the negligible contribution provided by in-stream refugia because of the drought intensity and length. Unlike other studies, where pools and the hyporheic zone have been recognized to be primary drivers of the post-drought recovery of benthic organisms (Vander Vorste, Malard, & Datry, 2016; Verdonschot et al., 2015), the prolonged drying conditions here observed probably nullified the suitability of such refugia. Indeed, pools disappeared in our intermittent sites and also the survival of macroinvertebrates in the moist interstitial spaces appears unlikely under similar circumstances. To confirm this, data acquired by a piezometer showed that, in the intermittent site of the Po river, water was 2.5 m below the ground level for the majority of the time from July to December 2017 (unpublished data, see Supplementary Materials Fig. SM2). Our results showed that the passive recolonization by drift from the upstream section was probably the main factor facilitating the recovery of macroinvertebrates in Alpine streams, according to the results of other authors (Doretto et al., 2018; Flower, 2004).

However, marked differences were found among the two examined lotic systems, thus supporting the role of recruitment in macroinvertebrate community resilience to exceptional droughts. In the Pellice river we observed a progressive and significant increase in all the diversity metrics since the water resumption and multivariate analysis indicated a partial overlap in the community composition of permanent and intermittent sites. As water resumed in this river, no relevant changes in flow and environmental conditions were observed among sampling occasions. This aspect, combined with the shorter distance from the upstream nearest permanent site, probably explains the recovery dynamics here documented, as pointed out by other authors (Bogan, Boersma, & Lytle, 2015; Fritz & Doods, 2004). On the contrary, the rewetting process in the Po river was strongly influenced by the precipitation amount (Supplementary Materials Fig. SM1): after a steady raise in flow, the riverbed shrank over the time and dried completely around 45 days from the water resumption with flowing water that re-established only on the last sampling occasions. As a consequence, richness and density of macroinvertebrates generally peaked within the first 20 days and then collapsed, while even after 73 days the taxonomical composition of the intermittent and permanent sites was still different. In addition, also the greater distance between these two sampling stations probably explains why an appreciable recovery was not reached in this lotic ecosystem.

Van Looy et al. (2018) indicated also that the resource competition/facilitation plays an important role on the resilience after a disturbance of riverine communities. Although we did not assess directly the food availability and biotic interactions, temporal changes in the percentages of FFGs and ratio between scrapers and total collectors were examined. FFGs have been widely invoked to indirectly infer riverine ecosystem attributes and their use in biomonitoring is currently growing (Cummins et al., 2005; Doretto, Piano, Bona & Fenoglio, 2018; Merritt, Fenoglio & Cummins, 2017). Temporal patterns for FFGs were found for both rivers but, interestingly, significant variations in the ratio between scrapers and total collectors were observed only in the Po river. This ratio was here used as an indicator of the prevalence of autotrophy or heterotrophy, and our results suggest that probably the availability and quality of periphyton and organic matter were not influential factors in the Pellice river (Falasco et al., in preparation), while they affected, at least partially, the recolonization process in the Po river.

To conclude, this work stresses the importance of the recolonization by drift as the main mechanism for the post-drought recovery of macroinvertebrates in Alpine streams. This is in accordance with conceptual framework proposed by Van Looy et al. (2018), for which the recruitment from adjacent habitat sources is usually the main drivers of community resilience in connected river network. As the intermittent and permanent sites in this study were located few kilometers aside, we assume that this condition applied to our results. However, we also demonstrated that river-specific attributes, such as local climate conditions, hydrology and the distance from the nearest upstream perennial site can strongly influence the recovery process. Given the predicted increment in the frequency and magnitude of anthropogenic and climate droughts in the mountain areas, the results of this study offer important information for the management and conservation of Alpine streams and their biota.

Data Availability Statement (DAS)

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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495 **Tables**

496

497 Table 1. Geographical information of the sampling sites.

River	Site	Coordinates	% Natural areas	% Agricultural areas	% Urbanized areas	Elevation (m.a.s.l.)	Distance between stations (Km)
Po	Perennial	367119E; 4945951N	93	6	1	474	5.5
	Intermittent	372959E; 4943103N	89	10	1	246	
Pellice	Perennial	364293E; 4963123N	92	6	2	422	3.1
	Intermittent	366638N; 4964043E	92	6	2	378	

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500 Table 2. Scheme of the sampling activity. Date = sampling date, Days = days from the water return
501 in the intermittent sites.

Date	Days	Pellice sites		Po sites	
		Perennial	Intermittent	Perennial	Intermittent
12th January 2018	3	-	Sampling	-	Sampling
16th January 2018	7	-	Sampling	-	Sampling
19th January 2018	10	Sampling	Sampling	Sampling	Sampling
23th January 2018	14	-	Sampling	-	Sampling
30th January 2018	21	-	Sampling	-	Sampling
1st February 2018	23	-	Sampling	-	Sampling
9th February 2018	31	-	Sampling	-	Sampling
23th February 2018	45	-	Sampling	-	Dry
9th March 2018	59	-	Sampling	-	Sampling
22th March 2018	73	Sampling	Sampling	Sampling	Sampling

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504 Table 3. Statistics of the GAMs for the macroinvertebrate community. Int = intercept, SE = standard
505 error, z = z-value, t= t-value, River = studied rivers (i.e. Pellice, Po), χ^2 = Chi-square, F = F-value, P =
506 p-value. Significant values are in bold.

Metric	Int	SE	z	River	χ^2	P
Taxa richness	2.214	0.046	48.370	Pellice	3.895	**0.048**
				Po	5.208	0.129
Total density	7.661	0.062	123.000	Pellice	10.520	**0.020**
				Po	111.730	**<0.001**
EPT richness	1.791	0.057	31.650	Pellice	3.827	**0.050**
				Po	3.319	0.238
EPT density	7.171	0.062	115.000	Pellice	21.700	**<0.001**
				Po	121.500	**<0.001**
% Collector-gatherers	-0.735	0.035	-21.010	Pellice	347.500	**<0.001**
				Po	152.200	**<0.001**
% Filterers	-0.637	0.036	-17.500	Pellice	549.700	**<0.001**
				Po	261.000	**<0.001**
% Predators	-4.064	0.119	-34.150	Pellice	48.078	**<0.001**
				Po	4.839	0.188
% Scrapers	-1.076	0.036	-30.010	Pellice	61.030	**<0.001**
				Po	215.950	**<0.001**
% Shredders	-4.335	0.121	-35.940	Pellice	5.986	0.055
				Po	2.214	0.137
Metric	**Int**	**SE**	**t**	**River**	**F**	**P**
Scrapers/Total collectors	0.605	0.061	9.905	Pellice	0.406	0.527
				Po	4.193	**0.013**

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Figure captions

Fig. 1. Sampling sites and elevational range of the sub-basins of the Pellice and Po rivers.

Fig 2. PCA ordination plot. Labels indicate: river (Pe = Pellice, Po = Po), type of site (P = Permanent, I = Intermittent) and sampling occasion expressed as days from the water return. Ellipses represent standard deviations around the centroids of sampling sites of the two rivers (solid line = Pellice river, dashed line = Po river).

Fig 3. NMDS ordination plot. Symbols represent the type of site (I = intermittent, P = perennial) for each river. Colors represent the sampling occasions, indicated as number of days since the water return. Ellipses represent standard deviations around the centroids of sampling sites of the two rivers (solid line = Pellice river, dashed line = Po river).

Fig 4. Generalized Additive Models (GAMs) for (a) total taxa richness, (b) EPT richness, (c) total density of macroinvertebrates and (d) EPT density. Black lines represent the predicted values of the models, while the dashed lines represent 95% confidence interval.

Fig 5. Bars indicate the percentage of functional feeding groups in the (a) Pellice and (b) Po rivers on each sampling occasion, expressed as days from the water return. GAMs for the ratio between scrapers and total collectors during the rewetting phase (c): black lines represent the predicted values of the models, while the dashed lines represent 95% confidence interval.

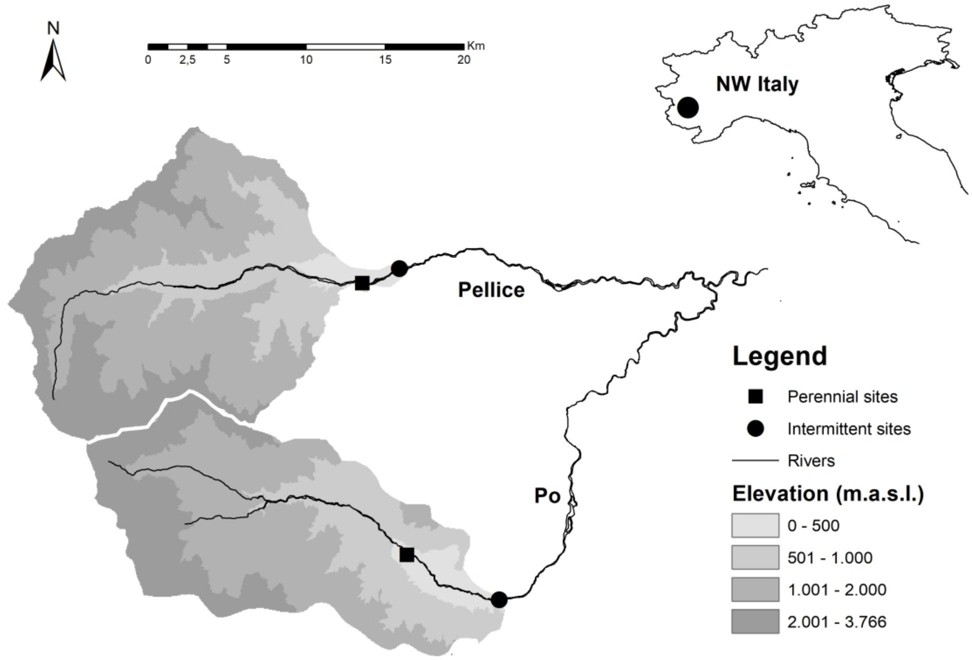

Fig. 1. Sampling sites and elevational range of the sub-basins of the Pellice and Po rivers.

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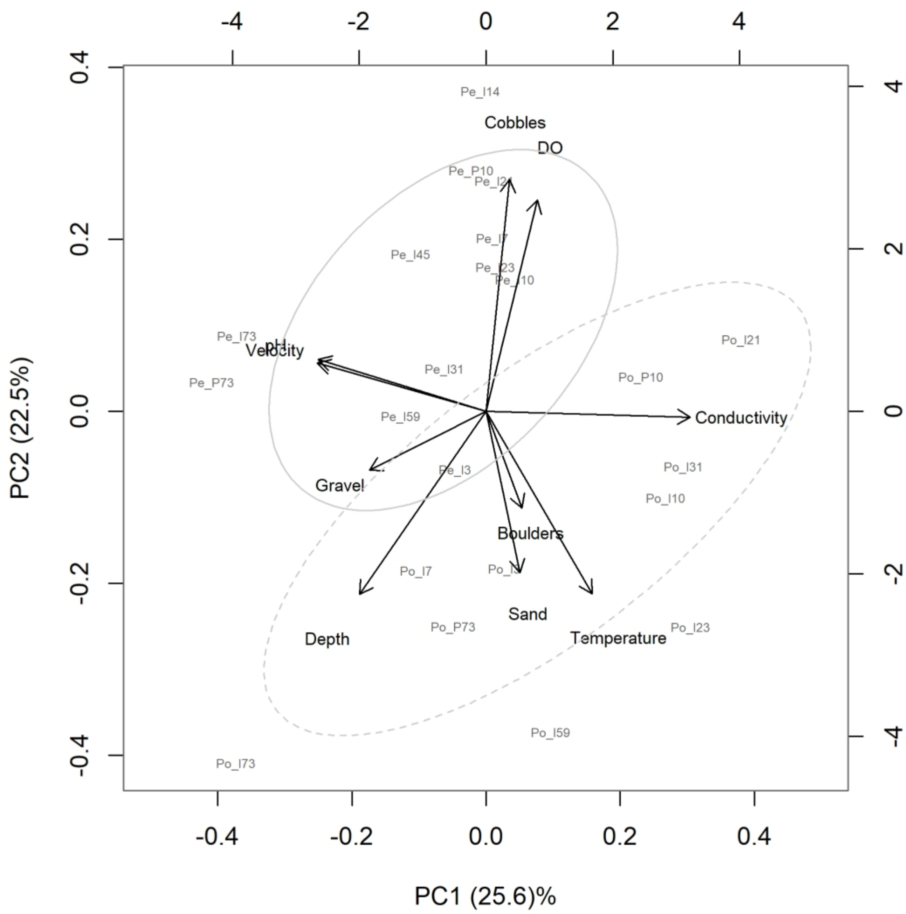

Fig 2. PCA ordination plot. Labels indicate: river (Pe = Pellice, Po = Po), type of site (P = Permanent, I = Intermittent) and sampling occasion expressed as days from the water return. Ellipses represent standard deviations around the centroids of sampling sites of the two rivers (solid line = Pellice river, dashed line = Po river).

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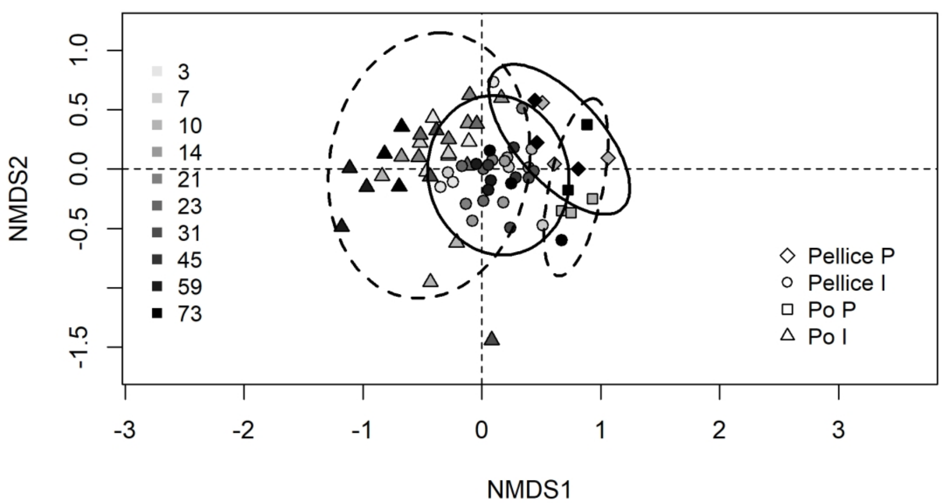

Fig 3. NMDS ordination plot. Symbols represent the type of site (I = intermittent, P = perennial) for each river. Colors represent the sampling occasions, indicated as number of days since the water return. Ellipses represent standard deviations around the centroids of sampling sites of the two rivers (solid line = Pellice river, dashed line = Po river).

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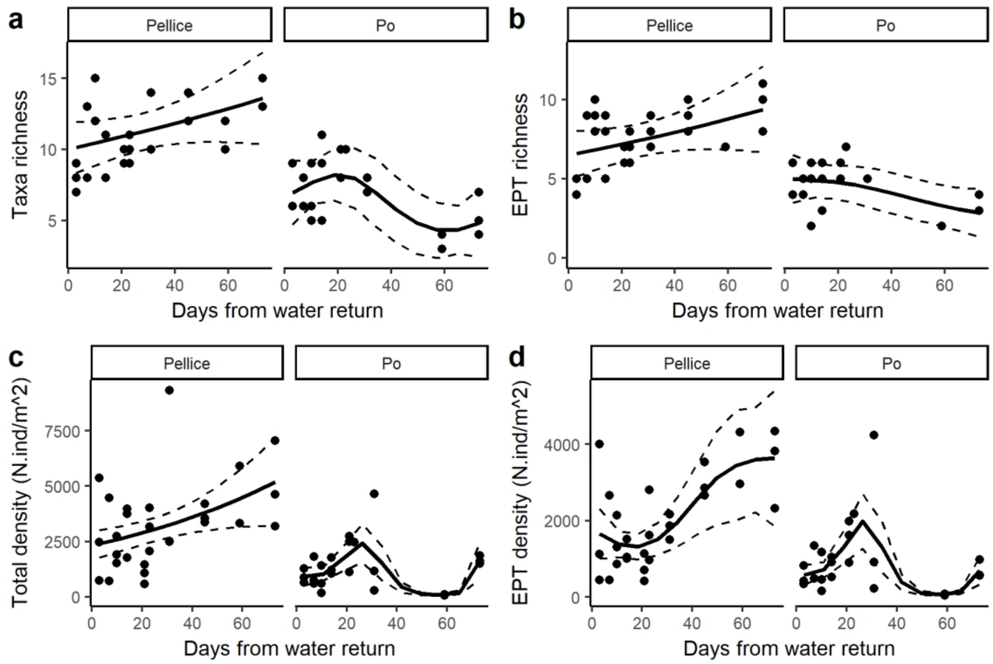

Fig 4. Generalized Additive Models (GAMs) for (a) total taxa richness, (b) EPT richness, (c) total density of macroinvertebrates and (d) EPT density. Black lines represent the predicted values of the models, while the dashed lines represent 95% confidence interval.

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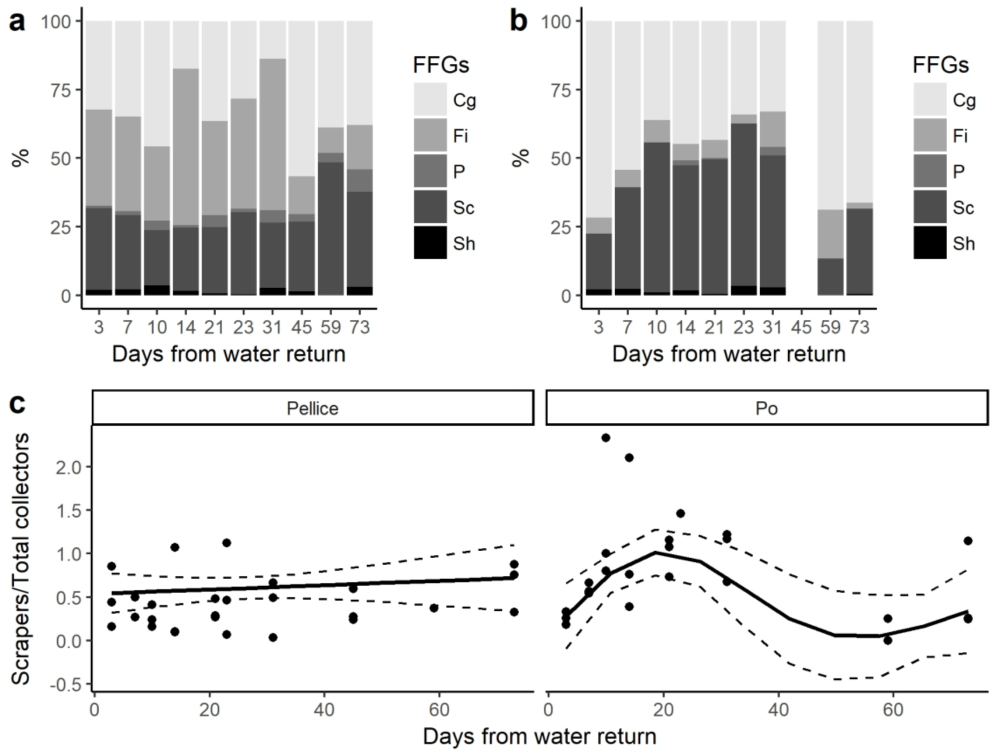

Fig 5. Bars indicate the percentage of functional feeding groups in the (a) Pellice and (b) Po rivers on each sampling occasion, expressed as days from the water return. GAMs for the ratio between scrapers and total collectors during the rewetting phase (c): black lines represent the predicted values of the models, while the dashed lines represent 95% confidence interval.

169x129mm (300 x 300 DPI)